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Experimental study of aggregation during the development of *Pseudosinella impediens* (Collembola, Entomobryidae)

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With 2 figures

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1. Introduction

In an earlier work the junior author studied the aggregation of various species of Collembola (CHRISTIANSEN 1970). The specimens used for this study were adults and subadults of varied age. The present study analyzes the change in aggregation, both general and about food, during the course of development of the cave species *P. impediens* GISIN et GAMA.

2. General aggregation — Methods and materials

Glass bowls 14.5 cm in diameter and 7.5 cm high with the bottom lined with cave clay to a depth of 1 cm were marked off into 6 equal divisions. Each division was numbered and had a piece of dry yeast placed in the center and the bowl was covered with a glass plate. Each bowl contained 15 animals and these were studied for five days. Each day the distribution of the animals was noted between 9—11 A.M. and again between 4—6 P.M. During the experiment the animals were kept in high humidity, total darkness and between 11 and 12 °C. Animals from each instar 1 to 5 were used and the animals placed in any one bowl were forms which had molted on the same day. Experiments involving each instar were repeated with different animals ten times.

3. General aggregation — Results

During each observation the number of animals on each subdivision was noted and these were grouped into frequency classes (i.e. 0 animal, 1 animal, 2 animals, etc.). The goal of this experiment was to see if the animals distributed at random or tended to aggregate. Any tendency toward aggregation could be measured as a departure from the Poisson distribution of these frequency classes with an increase in the categories 0 and 4 or more.

Table 1 presents the frequencies observed for each class and calculated on the Poisson series. On the basis of this data we graphed the expected frequency distribution on a Poisson series and the observed data for the first and fifth instar (see fig. 1A, B). There is an almost

Table 1. Frequencies observed (O) respectively calculated (C) for each class with the Poisson series

Class	Instar I		Instar II		Instar III		Instar IV		Instar V	
	O	C	O	C	O	C	O	C	O	C
0	98	85.50	101	79.85	105	79.19	118	79.86	126	80.66
1	162	166.59	165	161.04	158	160.37	152	161.05	160	161.86
2	148	162.29	126	162.39	131	162.37	127	162.39	119	162.40
3	114	105.30	102	109.16	99	109.15	97	109.15	74	108.62
4	41	51.33	64	55.03	61	55.48	56	55.03	54	54.49
5	22	20.00	27	22.19	26	22.47	27	22.19	46	21.87
6	11	6.49	10	7.46	16	7.58	13	7.46	11	7.31
7	3	1.80	4	2.14	4	2.94	6	2.14	8	2.09
8	1	0.61	1	0.74			2	0.54	2	0.70
9							2	0.19		
Total	600		600		600		600		600	

The classes 0, 1, 2 etc. represent the number of animals in each division. Each instar has two columns, the one on the left in each case represents the observed frequency (O) of the class and that on the right represents the calculated Poisson frequency (C).

perfect agreement between the two in the first instar whereas the fifth instar shows strong evidence of aggregations as measured by a departure from the Poisson distribution. This departure, barely visible in the 2nd instar increases regularly at each stage of development.

One of the characteristics of the Poisson distribution is the fact that its variance is equal to its mean. In our data this is clearly not so (see table 2). We did not count animals on the walls of the bowl or the cover and this accounts for the fact that the mean value is always lower than $15/6 = 2.5$. The difference between the variance and mean in the first instar is slight and can readily be explained, but after this there is a regular and increasing difference between the two. χ^2 [Chi²] values were calculated for each instar, lumping all classes above 6 into a single class. These χ^2 values are significant at the 5% level at instar II and below the 1% level at all instars from III on (see Table 2), and increase gradually during development (see fig. 1C).

Table 2. Comparisons of statistical data

Instar	I	II	III	IV	V
\bar{X} (Mean)	1.94	2.01	2.02	2.01	2.00
s^2 (Variance)	2.19	2.44	2.52	2.86	3.03
χ^2 (Chi square)	10.81	19.66	27.45	72.85	97.37

4. Aggregation around food — Methods and materials

The chambers used for these experiments were the same as for previous experiments; however, this time the six compartments were partially separated by glass plates so as to limit freedom of movement from one subdivision to another. The center of the chamber was undivided allowing some movement from one subdivision to another. Yeast was placed in only one subdivision, the one labelled A in each case. Ten animals were placed in each bowl and their movements recorded twice a day as before. As before the experiments were repeated ten times for each of instars 1—5 just as before. The goal of this test was to see if there was any change in food aggregation tendency during development.

5. Aggregation around food — Results

Table 3 illustrates the mean number of animals found in the food compartment during each instar. A tendency for diminution in food aggregation with age is clearly visible. While the t-test did not show any significant difference between any two sequential stages it was

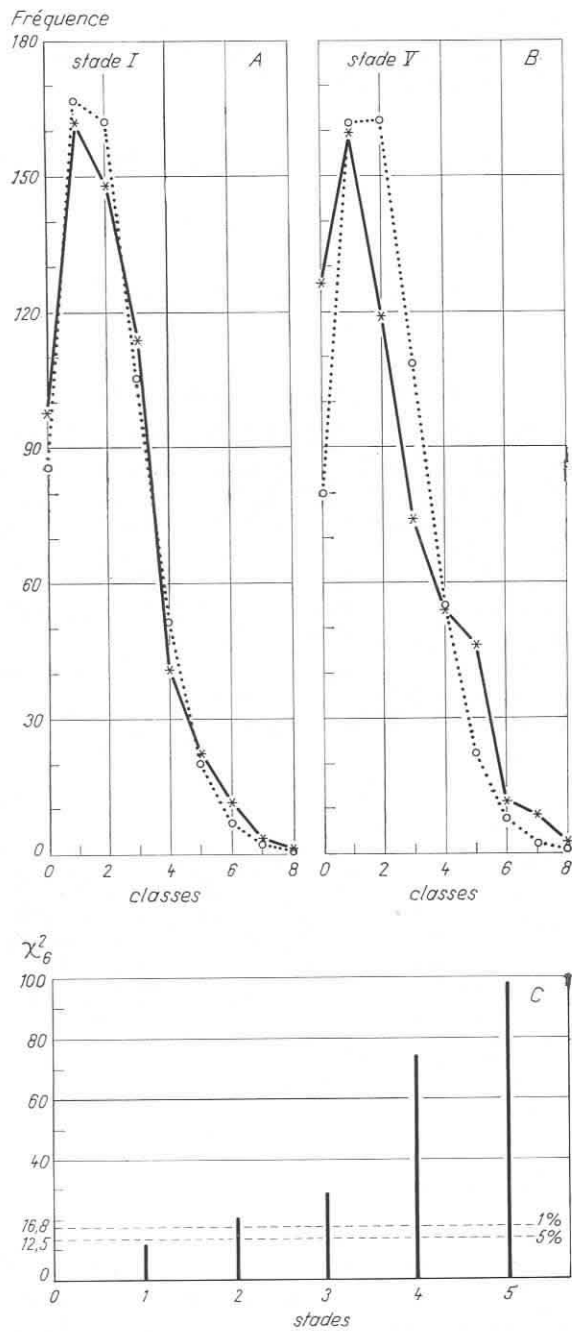


Fig. 1. General aggregation in *Pseudosinella impediens*. (A) Polygon of frequencies during the first instar. Full line indicates the number of Collembola per division and dotted line the Poisson's series adjusted to the observations. (B) Polygon of frequencies during the fifth instar. (C) χ^2 [Chi²] evolution in relation to the different instars.

significant between Instar 1 and Instar 5 (t 2.54 $P < 0.02$). In addition comparing the means of the food compartment with those of non-food compartments showed a highly significant difference in all stages ($P < 0.001$).

Table 3. Mean number of animals found in the food compartment A during different instars

Instar	I	II	III	IV	V
Compartment A					
\bar{X} (with food)	3.45	3.37	2.93	3.06	2.84
S.E. \bar{X}	(± 0.20)	(± 0.22)	(± 0.10)	(± 0.17)	(± 0.17)

6. Discussion and conclusions

Microarthropods of the soil can be distributed at random or in aggregations (VANNIER and CANCELA DA FONSECA 1966). The tendency for Collembola to form aggregations is well documented but its biological significance is poorly understood. Earlier studies have suggested that aggregations may be the result of cover area and other physical factors (JENSEN and CORBIN 1966) weak movement of the young and favorable microclimate (HALE 1966) or movement to optimal environmental conditions (JOSSE 1970). None of these serve to adequately explain the present results. An alternative explanation would rest on the adaptive value of aggregation or dispersion in different environments.

The junior author (CHRISTIANSEN 1970) offered evidence that there is a regular and adaptive change in behaviour as we move from endogeic to troglophile or marginal cave habitats to troglitic or cave depth habitat (see figure 2).

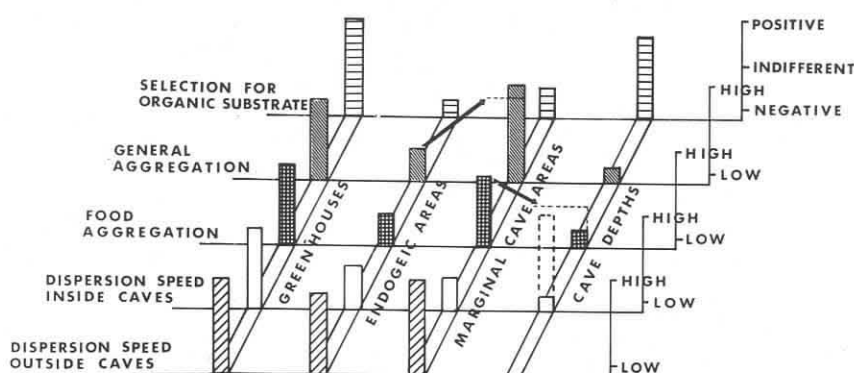


Fig. 2. Behavioural characteristics of Entomobryinae in different habitats. Arrows show the changes seen in *Pseudosinella impediens* during growth.

In both general aggregation and aggregation around food the endogeic habitat and troglitic habitat show little aggregation while the troglophile or cave margin habitat shows strong aggregation. *P. impediens* is so far only reported from caves; however, it shows little physical cave adaptation and is not an inhabitant of cave depths. The behaviour of *P. impediens* changes during growth from little to much general aggregation and shows a slight decrease in food aggregation. One possible explanation for this difference could be that the changes in behaviour seen during growth are recapitulative of the evolutionary changes of the organism. If this is so then the two aspects of behaviour are asynchronously changing towards increased cave adaptation (see arrows in figure 2). It would be possible to test this hypothesis by studying the behaviour of other species at different levels of adaptation.

The techniques used in this study allow the researcher to analyze behaviour in fashion which is repeatable and susceptible of sharp statistical analysis. The earlier studies showed that behaviour could be categorized on both taxonomic and ecological bases. The present study shows that there is a clear cut and regular change in behaviour with development. It is further suggested that this change may be a recapitulative phenomenon with the earlier growth stages reflecting earlier stages in the organism's evolution. Other explanations such as a shift in adaptive values with growth stage are also possible. Experiments could easily be designed to test each of these hypotheses.

7. Acknowledgements

We wish to thank Mme. J. DAFFIS for her very effective technical help during the course of this work. Preparation of the manuscript was supported by N.S.F. Grant 37677.

8. Summary . Résumé

The general and food aggregation tendencies of the Collembola *Pseudosinella impediens* were tested under stable cave conditions of no light, high humidity, and fixed temperature (12—11 °C). The technique were similar to those of CHRISTIANSEN 1970. Organisms were tested at each instar from I to V. It was found that there was a striking increase in general aggregation and a somewhat less striking decrease in food aggregation. It is suggested that these changes may recapitulate the evolutionary history of habitat change in this species. The study demonstrates the repeatability of behavioural tests of this sort.

Etude expérimentale de l'aggrégation au cours du développement postembryonnaire chez *Pseudosinella impediens*

Les aptitudes du Collembole *Pseudosinella impediens* à l'aggrégation générale et à l'aggrégation autour de la nourriture ont été analysées dans des conditions très proches de celles du milieu cavernicole : obscurité, forte humidité et température constante (11—12 °C). Les techniques et la méthodologie sont identiques à celles mises en œuvre par CHRISTIANSEN (1970). L'étude a été faite sur des individus de même âge, des stades I à V. On a constaté que la tendance à l'aggrégation au cours du développement se traduit par une forte augmentation dans le cas de l'aggrégation générale et par une diminution un peu moins importante dans l'aggrégation autour de la nourriture; il est possible que ces modifications traduisent l'histoire évolutive de cette espèce après son changement d'habitat. Ces études démontrent le caractère reproductible de ces tests de comportement.

9. References

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